

Bibliography of studies on hybrid zones of the common shrew chromosome races distributed in Russia

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Abstract

The common shrew, *Sorex araneus* Linnaeus, 1758, has become a model species for cytogenetic and evolutionary studies after discovery of extraordinary Robertsonian polymorphism at the within-species level. Development of differential staining techniques (Q-, R- and G-banding) made it possible to identify the chromosomal arms and their combination in racial karyotypes. Entering into contact with each other, the chromosomal races might form hybrid zones which represent a great interest for understanding of the process of speciation. Until recently all known hybrid zones of *S. araneus* were localized in Western Europe and only one was identified in Siberia (Russia) between Novosibirsk and Tomsk races (Aniskin and Lukianova 1989, Searle and Wójcik 1998, Polyakov et al. 2011). However, a rapidly growing number of reports on discovery of interracial hybrid zones of *Sorex araneus* in the European part of Russia and neighboring territories appeared lately. The aim of the present work is to compile the bibliography of all studies covering this topic regardless of the original language and the publishing source which hopefully could make research data more accessible to international scientists. It could also be a productive way to save current history of *Sorex araneus* researches in full context of the ISACC (International *Sorex araneus* Cytogenetics Committee) heritage (Searle et al. 2007, Zima 2008).

Keywords

Chromosome races, Hybrid zones, Robertsonian variation, *Sorex araneus*

Introduction

The common shrew, *Sorex araneus* Linnaeus, 1758, displays exceptional variability of karyotype derived from intraspecific chromosome rearrangements of the Robertsonian type. Metacentric pairs of *S. araneus* are formed by fusion of originally acrocentric chromosomes at their centromeres in different combinations of arms. As a result, the chromosomes number ($2n$) varies from 20 to 33, the odd number is due to the presence of karyotype of the Robertsonian heterozygote with one metacentric and two acrocentrics, instead of two homozygous metacentrics or four acrocentrics. At the same time the fundamental number of chromosome arms (FN) remains unchanged and is equal to 40. As far as this process takes place within populations, we could talk about Robertsonian polymorphism which occurs in the vast range of *S. araneus* species.

After the pioneer analysis in Western Europe in the 1950s and 1960s, the studies of Robertsonian polymorphism in *S. araneus* populations started in Russia, widening the area of cytogenetic investigations to include European and Asian parts of the former USSR (Orlov 1974). The observed variations in chromosome arm lengths led to conclusion that Robertsonian fusions might involve different arms in different populations, which resulted in widely varying non-homologous metacentrics (Orlov and Kozlovsky 1969, Ford and Hamerton 1970, Hausser et al. 1985).

Introduction of new methods of chromosome identification (Q-, R- and G-banding) improved the karyotype definition and increased the interest in the common shrew chromosome evolution. The International *Sorex araneus* Cytogenetics Committee, ISACC was founded at Oxford University in 1987 and until recently international meetings were held every 3 years. The results of its activity were summarized in 2007 by Searle et al. Based on chromosome specific G-banding patterns, Searle et al. (1991) established the standard nomenclature for chromosomes of *S. araneus*. Later rules for differentiation of the intrapopulation variants (polymorphism) from the interpopulation ones (polytypy) as well as from individual karyotype forms were developed (Hausser et al. 1994). Chromosome identification made it possible to describe the chromosomal races of *S. araneus* (Halkka et al. 1974, 1987). Results of karyological studies over the full species range were successively summarized first by Zima et al. (1996) and then by Wójcik et al. (2003). In Russia G-banded chromosomes of the common shrew were first described for a Siberian (Novosibirsk) population by Král and Radjabli in 1974. Results of further studies of high resolution G-banding and chromosome painting of race Novosibirsk represented the species in the international “Atlas of Mammalian Chromosomes” (2006) and in comprehensive comparative studies of *Sorex* (Biltueva et al. 2011). This race was also used for DAPI karyotyping of the common shrew (Minina et al. 2007).

Currently, no less than 72 chromosomal races are recognized in total (White et al. 2010). The number of Russian chromosomal races has already reached 25 (Orlov et al. 1996, 2007, Bulatova et al. 2000, Shchipanov et al. 2009, Pavlova 2010). Only four of these races are common for Russia and some neighboring areas. They include the following: 1) the Neroosa race which spreads over the southern regions of Russia and

Ukraine; 2) the West Dvina race which can be found in Russia – Belarus neighboring regions; 3) the Goldap race which inhabits the Baltic coast area of Poland and Kaliningrad region of western Russia; 4) the Ilomantsi race which occurs in the bordering areas of north-western Russia (Karelia) and Finland (Orlov et al. 1996, 2007, Bulatova et al. 2000, Shchipanov et al. 2009, Borisov et al. 2009a). As anticipated, regular studies of distribution of different races resulted in discoveries of interracial zones of contact in Russia (Shchipanov et al. 2009, Orlov et al. 2012, Pavlova 2013, Shchipanov and Pavlova 2013) and neighboring territories (Borisov et al. 2010, 2013). Due to ISACC activity, research that involves detection of the hybrid zones, as well as discovery and description of the chromosome races continues on a regular basis.

The first case of *S. araneus* interracial hybridization in Russia was presented by Aniskin and Lukianova (1989) for Tomsk and Novosibirsk races in Western Siberia. This hybrid zone is characterized by the high number of the chromosome arm combinations and remains one of the most complex and best studied *S. araneus* hybrid zones (Searle and Wójcik 1998, Polyakov et al. 2011). The hybrids here form a complex meiotic configuration, a long chain of 9 monobrachially homologous acrocentrics and metacentrics. Presumably, chromosome incompatibility proved by meiosis data may induce infertility in hybrids which, in turn, could contribute to promotion of the selection for assortative mating (Searle and Wójcik 1998). Given that racial karyotypes of *S. araneus* as a rule differ by 1–5 variable metacentrics, the hybrids should produce rings or chains of different numbers and length in meiosis. Thus, the simplest heterozygotes form the chain of three, CIII, or ring of four, RIV. The most complex heterozygote was registered in Moscow and Seliger races hybrids in European Russia, and represents the chain of eleven, CXI (Bulatova et al. 2007). As far as the meiotic complications may lead to reduced hybrid reproductive fitness, the incompatibility is to be considered as the first stage in reproductive isolation. There are indications that the Robertsonian rearrangements do not interrupt the existent gene flow in hybrid zones and could not promote speciation in *S. araneus*. Instead, races might be merely remnants of past allopatric differentiation followed by the loss of secondary contact (Horn et al. 2012, Polly et al. 2013), presenting in particular astonishing racial ‘patchwork’.

As has been shown in a variety of recent studies, the number and diversity of the chromosome rearrangements along with the relative variety of hybrid zone types represent a great opportunity both for understanding of the aftereffects and possible connections of chromosome mutations with the morphological, ecological and genetic differentiation in wild populations of common shrews (see Bibliographic list). It seems quite appropriate to recall the forecast made the British cytogeneticists CE Ford and JL Hamerton in 1970 (p. 235): “... shrews displayed multiple patterns of chromosome variation predicting the problems essential for the interpretation of species evolution. Information about hybrid meiosis would be of outstanding value and studies of pregnant females and their embryos from polymorphic populations could give important information about the breeding system and relative fertility. At a more modest level there remain many parts of Europe from which simple identification of the karyotype in samples from the local population could at least help to fill in the still rather

fragmentary distribution map of Races A and B and might reveal further unsuspected chromosome variation”. Till now only the second part of this task has been mostly accomplished, while our knowledge of the influence of chromosome rearrangements on cells, specimen and species is still too fragmentary.

The first tribute to the bibliography on the *S. araneus* cytogenetic model was paid by Prof. Jan Zima at the 8th ISACC meeting (2008). To support his idea, we compiled the bibliographical list which includes majority if not all of currently available papers devoted to interracial hybrid zones of *S. araneus* in Russia. The Bibliographic list presented here includes 43 full papers published in national and international scientific editions within the last 40 years. As it shown by the published data, hybrid karyotypes and true hybrid zones were reported for at least 14 out of 25 chromosome races (which are indexed below) of the common shrew that inhabit Russia. This index includes the names of the races and their standard abbreviations, karyotypic diagnosis and F1 hybrids meiotic formula followed by the reference number of the relevant papers from our Bibliographic list.

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*Papers from the Bibliographic list referred to in the Introduction and not included in the final References are marked with asterisks.

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Index

Kirillov (Kr)

gm, hi, kq, no, pr

- Manturovo (F1: gm/mn/no/go, hi, kq, pr; RIV): 22, 43

- Petchora (F1: gm/gi/hi/hn/no/mo, kq, pr; RVI): 39, 43

Manturovo (Ma)

go, hi, kq, mn, pr

- Kirillov (F1: gm/mn/no/go, hi, kq, pr; RIV): 22, 43

- Petchora (F1: gi/hi/hn/mn/mo/go, kq, pr; RVI): 43

- Sok (F1: go, kq, hi/ip/pr/mr/mn/hn; RVI): 43

Moscow (Mo)

gm, hi, kr, no, pq

- Neroosa (F1: gm/go/no/mn, hi, kr, pq; RIV): 17, 24
- Seliger (F1: g/gm/mq/pq/pr/kr/ik/hi/hn/no/o; CXI): 1, 6, 8, 10, 15, 21, 23, 25, 26, 27, 29, 40, 41, 42
- West Dvina (F1: gm, hi/ip/pq/qr/kr/hk, no; RVI): 6, 18, 20, 21, 23, 40

Neroosa (Ne)

go, hi, kr, mn, pq

- Moscow (F1: gm/go/no/mn, hi, kr, pq; RIV): 17, 24

Novosibirsk (No)

go, hn, ik, mp, qr

- Tomsk (F1: o/go/gk/ik/hi/hn/mn/mp/p, qr; CIX): 1, 11, 15, 16, 28, 29, 30, 31, 32, 34, 35, 36, 38
- Serov (F1: go, hn, ik/ip/mp/km, qr; RIV): 28, 33

Petchora (Pt)

gi, hn, kq, mo, pr

- Kirillov (F1: gi/hi/hn/no/mo/gm, kq, pr; RVI): 39, 43
- Serov (F1: gi/go/mo/km/kq/qr/pr/ip, hn; RVIII): 43
- Sok (F1: gi/go/mo/mr/pr/ip, hn, kq; RVI): 43

Seliger (Sl)

g, hn, ik, mq, o, pr

- Moscow (F1: g/gm/mq/pq/pr/kr/ik/hi/hn/no/o; CXI): 2, 6, 8, 10, 15, 21, 23, 25, 26, 27, 29, 40, 41, 42
- West Dvina (F1: g/gm/mq/qr/pr/ip/ik/hk/hn/no/o; CXI): 20

Serov (Se)

go, hn, ip, km, qr

- Novosibirsk (F1: go, hn, ik/ip/mp/km, qr; RIV): 28, 33
- Petchora (F1: gi/go/mo/km/kq/qr/pr/ip, hn; RVIII): 43
- Sok (F1: go, hn, ip, km/mr/qr/kq; RIV): 43
- Yuryuzan (F1: go, hn, ip, km/mq/qr/kr; RIV): 40, 43

Sok (So)

go, hn, ip, kq, mr

- Manturovo (F1: go, kq, hi/ip/pr/mr/mn/hn; RVI): 43
- Petchora (F1: gi/go/mo/mr/pr/ip, hn, kq; RVI): 43
- Serov (F1: go, hn, ip, km/mr/qr/kq; RIV): 43



Figure 1. Schematic view of geographic distribution (slash) of hybrid zones between chromosome races of *Sorex araneus* in Russia. Standard abbreviations are used for the racial names (see Index).

Strelka (Sr)

go, hi, k, m, n, p, q, r

- Tomsk (F1: k/gk/go/o, hi, q/r, m, n, p; CIV): 28, 37

Tomsk (To)

gk, hi, mn, o, p, qr

- Novosibirsk (F1: o/go/gk/ik/hi/hn/mn/mp/p, qr; CIX): 1, 11, 15, 16, 28, 29, 30, 31, 32, 34, 35, 36, 38

- Strelka (F1: k/gk/go/o, hi, q/r, m, n, p; CIV): 28, 37

West Dvina (Wd)

gm, hk, ip, no, qr

- Moscow (F1: gm, hi/ip/pq/qr/kr/hk, no; RVI): 6, 19, 20, 21, 23, 40

- Seliger (F1: g/gm/mq/qr/pr/ip/ik/hk/hn/no/o; CXI): 20

Yuryuzan (Yu)

go, hn, ip, kr, mq

- Serov (F1: go, hn, ip, km/mq/qr/kr; RIV): 40, 43

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